Pleistocene bird remains from Tornewton Cave and the Brixham Windmill Hill Cave in south Devon

C. J. O. Harrison

Subdepartment of Ornithology, British Museum (Natural History), Tring, Herts

Synopsis

Avian fossil material has been found in Tornewton Cave and the Windmill Hill Cave at Brixham, both in south Devon, England. The Tornewton material originates from strata deposited during an early cold phase, followed by an Ipswichian warm phase and by cold Devensian phases. The Brixham Cave material is Devensian in age. Twenty-two bird species are identified, including a new species of small partridge *Alectoris sutcliffei*. The abundant remains of the Shelduck *Tadorna tadorna* are thought to have been prey of the White-tailed Sea-eagle *Haliaeetus albicilla*, and their absence from Tornewton in the Devensian may be because of the absence of the predator rather than the prey species. Because many species are migratory, birds are often poor indicators of climatic conditions. Apart from the presence of Ptarmigan *Lagopus mutus* in the Devensian, the tundra species are absent. It is suggested that parts of the area may have carried a more boreal flora during the cold periods, and that the area may have benefited from the proximity to the sea which may have had some modifying effect on climatic conditions.

Introduction

The caves of south-west England have yielded a large quantity of late Pleistocene remains of mammals and birds, with the former in greater abundance. Unfortunately in some caves an accidental admixture of earlier deposits with Recent material during the later stages of deposition or during animal or human occupation, and the collecting of some specimens in the last and the early part of the present centuries without due regard to stratification of the cave floor, have made the contents of these caves of limited value in the study of faunal succession at different periods.

Tornewton Cave is an exception in that careful collecting of material during nearly two decades makes it possible to study a succession of specimens dating from the last, Devensian glaciation back through a warm period of the Ipswichian interglacial to a preceding cold period (Sutcliffe & Zeuner 1962). This cave provides the main mass of material, and the more limited material from the Windmill Hill Cave has been included because this is from the last glaciation, of Devensian age, and supplements the information provided by the Tornewton specimens for this period. All the material consists of dissociated bones, and mainly of the ends of the larger limb bones.

All the specimens referred to are in the collection of the Department of Palaeontology of the British Museum (Natural History); numbers prefixed with A or without prefix. The Windmill Hill Cave at Brixham was excavated by W. Pengelly in 1858–9 and the specimens collected were presented, mainly by the Royal Society, in 1876. The Museum purchased from F. H. Butler part of the collection made by J. L. Widger at the Tornewton and other Torbryan Caves (Walker & Sutcliffe 1967) in 1892, and the eagle claws from this have been included. The remaining extensive Tornewton material was collected in the period 1944–69 and presented by the late Mr S. R. Willing.

The Brixham Cave specimens were identified by Lydekker (1891). Some of the earlier Tornewton material had been identified by Miss P. Lawford in 1955, and some Glutton Stratum bones by D. Bramwell in 1961. The material from this cave had also been examined more recently by Dr J. Janossy of Hungary. For the present paper the material was critically re-examined and compared with Recent osteological specimens in the Sub-department of Ornithology, British Museum (Natural History) and reidentified where necessary.

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Sites and strata

Tornewton Cave is one of a series of caves in the limestone on the west side of the Torbryan Valley in south Devon. It is about 250 ft (76 m) above sea level, and about five miles (8 km) from the sea at Torbay to the east of it, and about six and four miles (9·5 and 6·5 km) from the upper ends of the estuaries of the rivers Teign and Dart respectively. The Windmill Hill Cave at Brixham is on a hillside bordering the coast on the south side of Torbay, the cave now being within the town of Brixham. The position of the coastline would have differed from that of the present day during the various cold and warm periods of the Pleistocene. In cold periods it would have been much further away, and maps reconstructing the distribution of the icefields sometimes tentatively indicate a coastline from south-western Ireland to beyond Brittany. From the present altitude of the surrounding areas, in warm periods the coast might not have been much closer to the cave than it is at present. However, the preponderance of Shelduck bones in most strata of the caves implies that conditions suitable for this species were present no further away than the distance which a predator was likely to transport them. Unless their ecological requirements differed significantly at this period, Shelduck would have required saline or brackish mudflats on which to feed, such as usually occur along estuaries or around lagoons with fluctuating water levels.

The sequence of deposits in Tornewton Cave has been studied and named with reference to the mammal fauna (Sutcliffe & Zeuner 1962). Both the mammal remains and the nature of the deposits indicate that the latter were laid down in several different climatic periods. They commence in an earlier cold period, which is overlain by a more typically warm Ipswichian deposit, and the most recent of the Tornewton deposits are from the last, Devensian, glaciation. The whole series of deposits referred to in the present paper, beginning with the earliest, is as follows.

Tornewton Cave

Glutton Stratum (? late Wolstonian or later cold phase). This deposit, so named because it contains remains of the Wolverine or Glutton, *Gulo gulo*, was laid down during a cold period with a severe climate and also contains remains of other northern mammals such as Reindeer, *Rangifer tarandus*. This may have been the later stage of the Wolstonian (penultimate) glaciation, but since there may have been one or more cold stages in the last interglacial interval (Shackleton 1969, 1977; Sutcliffe 1975, 1976; Woillard 1978) this cannot be established with certainty.

Bear Stratum (? late Wolstonian or later cold phase). This has a similar fauna to the Glutton Stratum, but with some evidence from the nature of the deposits of an ameliorating climate, cool but not as cold as the previous one.

Otter Stratum (?). This stratum occurs in a small side chamber of the cave. The otter referred to is the extinct clawless otter *Cyrnaonyx antiqua*, also occurring in the Glutton Stratum but not otherwise known in Britain. The stratum appears to consist of a mixture of two deposits, one warmer and the other cooler, and to have been deposited in a period between the Glutton Stratum and Hyaena Stratum depositions, with elements of both (Sutcliffe & Kowalski 1976).

Hyaena Stratum (Ipswichian Interglacial). The fauna is that of a warm interglacial period.

Reindeer Stratum (Devensian). The mammalian fauna of this period indicates a return to glacial conditions; Man was present. An earlier Devensian cold stage is represented at the cave by 'the Head', a deposit from which no bird material has been collected.

'*Eboulis*' (Devensian). The position of this deposit in the sequence of strata is not completely certain, but it may represent another later phase.

Windmill Hill Cave, Brixham

(Devensian). The material from this cave has not been assigned to a series of strata.

The bird species identified, dating from the Devensian glaciation back to an earlier cold phase, have been tabulated by strata (Table 1); to aid comparison the occurrences for the earlier and later cold periods have, in addition, been grouped in single columns on either side of the list for the single warm period between.

Table 1 Occurrence of species identified

Species	Glutton Stratum (cold)	Glutton/ Bear (cold)	Bear Stratum (cool)	Otter Stratum (?)	Combined early (cold)	Hyaena Stratum (warm)	Combined Late (cold)	Reindeer Stratum (cold)	'Eboulis' Stratum (cold)	Brixham Cave (cold)
? White Stork	×	×	×	–	×	–	–	–	–	–
Brent Goose	–	–	–	×	×	×	–	–	–	–
? Ruddy Shelduck	–	–	–	–	–	×	–	–	–	–
Common Shelduck	×	×	×	×	×	×	×	–	–	×
Wigeon	–	–	–	–	–	×	–	–	–	–
Teal	–	–	–	–	–	–	×	×	–	–
Goosander	×	–	–	×	×	–	–	–	–	–
White-tailed Sea-eagle	–	–	?×	–	?×	–	–	–	–	–
Common Buzzard	–	–	–	–	–	–	×	–	–	×
Kestrel	×	–	–	–	×	×	–	–	–	–
Ptarmigan	–	–	–	–	–	–	×	×	×	–
Willow Grouse	–	–	–	–	–	–	×	×	–	–
Western Partridge (sp. nov.)	×	–	–	–	×	–	–	–	–	–
Little Bustard	–	–	–	–	–	–	×	×	–	–
Eagle Owl	×	–	–	–	×	–	–	–	–	–
Skylark	–	–	–	–	–	×	×	×	–	–
Tree Pipit	–	–	–	–	–	×	–	–	–	–
Fieldfare	–	–	–	–	–	–	×	×	–	–
Crossbill	×	–	–	–	×	–	–	–	–	–
Starling	–	–	–	–	–	×	×	×	–	–
Carrion Crow	–	×	–	–	×	–	×	×	–	–
Raven	×	–	–	–	×	×	–	–	–	–

Systematic list of material

? WHITE STORK, *Ciconia ? ciconia*. Two very similar species of stork occur in the Palaearctic today, the White Stork and the Black Stork *C. nigra*. Both occur in marshy habitats, the former in more open country and the latter in forest. Osteologically they are very similar, but with some differences in the proportional lengths of limb bones. Since the fossil specimens are broken ends of bones these differences cannot be used. Three Recent *C. ciconia* specimens and two of *C. nigra* were available for comparison. The fossil specimens agree with those of *C. ciconia* in having on the distal end of the tibiotarsus a broader anterior tendinal canal and a narrower tubercle on the tendinal bridge.

The material comprises parts of carpometacarpi, radii, tarsometatarsi and tibiotarsi from the Glutton Stratum, a distal end of a tibiotarsus from the Glutton/Bear Stratum transitional zone and part of a radius from the Bear Stratum. A4095, A4110, A4117, A4118, A4135, A4143, A4166.

BRENT GOOSE, *Branta bernicla*. Bone fragments of this species are sometimes difficult to separate from those of *Tadorna* spp., but the present specimens can be assigned to it. The material comprises parts of tarsometatarsus and humerus from the Otter Stratum and parts of carpometacarpus, ulna and radius from the Hyaena Stratum. A4107, A4127, A4154, A4157.

COMMON SHELDUCK, *Tadorna tadorna*. Bones referable to this species form the major part of the whole collection. When Lydekker (1891) examined the Brixham material he does not appear to have used a specimen of this species for comparative purposes, although one was present in the Museum collection at the time. He compared the bones with those of the Ruddy Shelduck *T. ferruginea* and the South African Shelduck *T. cana*. He seemed unaware that there is a strong sexual dimorphism in the present species, the female being smaller, and he suggested that the smaller specimens represented a new species. Possibly because of these comments most of the shelduck material in the collection of the Department of Palaeontology had been tentatively assigned to *T. ferruginea*. Skeletons of three *T. tadorna* and five *T. ferruginea* were available for comparison. Differences in the limb-bones are slight, but in general *T. tadorna* has shorter and stouter bones and, with one exception, where differences were apparent the material was referred to this species. Humerus, tarsometatarsus and to a lesser degree the femur are the most useful bones for comparative purposes.

From the Tornewton Cave the material comprises tarsometatarsi, tibiotarsi, femora, coracoids, humeri, radii, ulnae, carpometacarpi, anterior ends of sterna, and furcula from the Glutton Stratum; tarsometatarsi, tibiotarsi, coracoids, humeri, ulnae, carpometacarpi, sacrum and vertebrae from the Glutton/Bear Stratum transitional zone; tarsometatarsi, femora, coracoids and ulna from the Bear Stratum; tarsometatarsi, tibiotarsi, femora, coracoids, humeri, radii, ulnae and carpometacarpus from the Hyaena Stratum; and tarsometatarsi, tibiotarsi, coracoids, ulnae and carpometacarpi from the Otter Stratum. A4091–3, A4096–7, A4099–4101, A4108, A4113–6, A4136, A4155–7, A4162–4, A4170, A5033–4, A5036.

From the Windmill Hill Cave, Brixham, we have tarsometatarsi, tibiotarsi, femora, coracoids, scapulae, humeri, ulnae, radii, carpometacarpi, metacarpal, anterior ends of sterna, furcula and vertebrae. 48911, 48915, A113, A3138–48, A3150–74, A3179–81.

? RUDDY SHELDUCK, *Tadorna ? ferruginea*. As mentioned above, there are difficulties in separating the bones of the two *Tadorna* species. The present specimen is a femur from the Hyaena Stratum, A5037, which is longer and proportionally more slender than any in the available skeletons of *T. tadorna*; it matches that of a male *T. ferruginea*. Specimens collected at the same time from the same stratum are referable to *T. tadorna*.

WIGEON, *Anas penelope*. Coracoid and part of a carpometacarpus from the Hyaena Stratum. A4111, A4124.

TEAL, *Anas crecca*. Femur, carpometacarpus and part of a humerus from the Hyaena Stratum. A4104, A4121, A4122.

GOOSANDER, *Mergus merganser*. Parts of humeri from the Glutton Stratum and parts of tibiotarsi and coracoids from the Otter Stratum. A4198, A4138, A5035.

WHITE-TAILED SEA-EAGLE, *Haliaeetus albicilla*. Claws, A233, collected by J. L. Widger and received with other Widger specimens, are merely labelled 'Torbryan Caves' but are very probably the ones referred to in his account (Walker & Sutcliffe 1967 : 80) as 'claws of an immense bird' and collected in the Bear Stratum of Tornewton Cave. There is also a single claw, A4141, from the Tornewton cave but from unstratified material.

COMMON BUZZARD, *Buteo buteo*. It is possible that the Rough-legged Buzzard *B. lagopus* may have occurred in this region in colder periods in view of its typical climatic and habitat preferences, but the present material is referable to the smaller *B. buteo*, the specimens matching those of the smaller male of this dimorphic species. The material comprises parts of humerus, ulna, carpometacarpus and pelvis from the Windmill Hill Cave, Brixham. 48913, 48917, A3149.

KESTREL, *Falco tinnunculus*. Parts of ulna and tarsometatarsus from the Glutton Stratum; coracoid, carpometacarpus and ulna from the Hyaena Stratum. A4133, A4149–51, A4159.

PTARMIGAN, *Lagopus mutus*. Several bones of this species are present, but the characteristic tarsometatarsi are a little smaller than those of Recent specimens. The material comprises parts of tarsometatarsi and coracoid from the Reindeer Stratum outside the cave, and part of a carpometacarpus from the 'Eboulis' deposit. A4125, A4147, A4148.

WILLOW GROUSE, *Lagopus lagopus*. A tarsometatarsus from the Reindeer Stratum outside the cave. A4106.

WESTERN PARTRIDGE, *Alectoris sutcliffei* sp. nov. See p. 96.

LITTLE BUSTARD, *Otis tetrax*. Part of a carpometacarpus from the Reindeer Stratum outside the cave. A4112.

EAGLE OWL, *Bubo bubo*. Although incomplete the specimen agrees in size with the larger northern Recent form of this species, whereas that from the earlier Cromer Forest Bed Series of East Anglia (Harrison 1979) is similar to the smaller southern Recent form. The material is an ungual from the Glutton Stratum. A4169.

SKYLARK, *Alauda arvensis*. An ulna, humeri and coracoid from the Hyaena Stratum; humeri, coracoids and carpometacarpi from the Reindeer Stratum. A4102, A4103, A4134, A4152.

TREE PIPIT, *Anthus trivialis*. There is little osteological variation among the pipits. Material is part of a humerus from the Hyaena Stratum. A4123.

FIELDFARE, *Turdus pilaris*. A coracoid from the Reindeer Stratum. A4192.

CROSSBILL, *Loxia* cf.*curvirostra*. The specimen resembles the corresponding bone of *L. curvirostra*, and is smaller and less stout than that of *L. pytyopsittacus*. *L. scoticus* is intermediate in general size between these two, and the Asiatic *L. leucoptera* is smaller than *L. curvirostra*, but comparative osteological material is not available. The breeding distribution of northern European crossbills is broadly linked with the occurrence of either Spruce or Pine trees, though birds may at times take seeds of either as well as of other conifers. Nethersole-Thompson (1975) has suggested that crossbills speciated from an ancestral form when their original principal foodsource, the Spruce *Picea abies*, ceased to occur, to produce the Scottish Crossbill *L. scoticus* and the Parrot Crossbill *L. pytyopsittacus* in Scandinavia and northern Russia, both specializing mainly on the seeds of the Scots Pine *Pinus sylvestris*. Further east the Common Crossbill *L. curvirostra* persisted as a specialist mainly on Spruce. The latter tree did not re-invade Europe after the last glaciation until after the isolation of the British Isles, where neither tree nor bird is native, although the first has been introduced and the latter has recently re-invaded and now breeds. From the evidence of pollen deposits Spruce did occur in Britain through the Pleistocene until the Lower Wolstonian, although in smaller proportions than other forest trees, and later as a scarce and probably localized tree in Ipswichian to Lower Devensian times, but not subsequently

(West 1977). The present specimen might therefore have been co-extant with Spruce in south-west England, and its normal existence was certainly correlated with the presence of conifers. The material is part of a humerus from the Glutton Stratum. A4128.

Starling, *Sturnus vulgaris.* On average these bones are slightly larger than those of Recent specimens. Two of the humeri are atypical in lacking the anconal fossa near the proximal end of the shaft. Carpometacarpi, ulnae, humeri, coracoid and femora are from the Hyaena Stratum; femora, coracoids, humeri, ulnae and carpometacarpi are from the Reindeer Stratum. A4105, A4130, A4139, A4140, A4144–6.

Carrion Crow, *Corvus corone.* The bones are towards the larger end of the size range of the species and the tibiotarsus shaft is stout. We have part of a tibiotarsus from the Glutton/Bear transitional zone and part of a femur from the Reindeer Stratum outside the cave. A4109, A4126.

Raven, *Corvus corax.* Parts of humeri, tibiotarsus and tarsometatarsus from the Glutton Stratum; ulna and parts of coracoids, tibiotarsus and tarsometatarsus from the Hyaena Stratum. A4031, A4044, A4119, A4120, A4132, A4142, A4160, A4161.

Systematic description

Order **GALLIFORMES**

Family **PHASIANIDAE**

Genus ***ALECTORIS*** Kaup, 1829

Alectoris sutcliffei sp. nov.

Western Partridge; Fig. 1

Diagnosis. Small, distal end of tibiotarsus smaller than that of any known *Alectoris* species.

Name. After Dr A. J. Sutcliffe, who has worked extensively on Pleistocene mammal remains and was responsible for assembling most of the present material.

Material. Holotype the distal end of a left tibiotarsus, collected by A. J. Sutcliffe in 1960; BM(NH) no. A4165. Tentatively referred specimen a distal end of a tibiotarsus (illustrated as a left-hand bone, but described in the caption as from the right) described by C. Mourer-Chauviré (1975) as '*Alectoris* sp.'.

Occurrence. Holotype from the Upper Middle Pleistocene; Glutton Stratum, Tornewton Cave, Torbryan, Devon, England. Tentatively referred specimen from ? Gunz glaciation, Early Middle Pleistocene; Mas Rambault à Frontignan, Hérault, southern France.

Description and discussion. The specimen is the distal end of a tibiotarsus of a small phasianid gamebird. It had tentatively been identified as that of a Common Partridge *Perdix perdix* but it is stouter with less anteriorly-prominent condyles and a wider and more anteroposteriorly-flattened shaft. It matches the tibiotarsi of *Alectoris* species but is smaller. Its width is 6·5 mm and that of the French specimen, calculated from the scale provided, is *c.* 6·75 mm. For the Red-legged Partridge, *A. rufa*, comparable measurements are 7·2–7·3 mm (5 specimens) and for the Rock Partridge *A. graeca*, Barbary Partridge *A. barbarae* and Chukar *A. chukar* they range from 7·4 to 8·5 mm (11 specimens). The species is therefore distinctly smaller than others of this genus. Mourer-Chauviré (1975) recognizes *A. graeca* and *A. barbarae* from cave deposits in southern France back to the Mindel glaciation, but finds no evidence of *A. rufa* which is now the native species of most of southern France. It is possible that the latter is derived from an Iberian isolate of fairly late glacial origin. The western zone of the range of *Alectoris*, including the southern site of *A. sutcliffei*, is now occupied by *A. rufa*, but the extinct *sutcliffei* occurred further north, and in a colder period, and must have been more tolerant of low temperatures.

MEASUREMENTS (in mm). Length of specimen 12·4; distal width 6·5; anteroposterior thickness of internal condyle 6·4, of intercondylar groove 3·8, of external condyle 5·8; width and thickness of shaft 4·5×2·7; distoproximal width of tendinal bridge 2·1.

The avian predators

The range of prey species found in caves is determined by the species of predator which fed there, and from the specimens examined in the present study it seems likely that avian predators were responsible for introducing most or all of the bird remains; they tend to leave bird bones relatively complete whereas mammalian predators tend to splinter and destroy them. Avian predators also tend to have a preferred prey size which may limit their range of prey significantly, and they may concentrate on some easily available species.

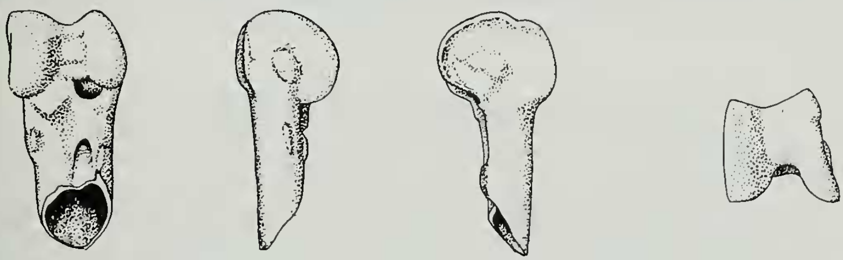

Fig. 1 *Alectoris sutcliffei* sp. nov. **Holotype**, distal end of left tibiotarsus, BM(NH) no. A4165. (Left to right) distal, internal, external, anterior views.

The predominant bird bones found were those of the Common Shelduck. This species presents two problems; it is a large and heavy prey for an avian predator, and a bird of estuaries and coasts. The coast is at present several miles from Tornewton Cave and is unlikely to have been much nearer the cave in the past. The Shelduck feeds on tidal mudflats. Although it may fly inland to utilize concealed nest sites, it is doubtful if this would explain the number of fossil remains. The presence at the same period of the Brent Goose, a similar large species of tidal mudflats, and possibly of the Wigeon which also occurs on this type of habitat in winter, tends to support the suggestion of a predator hunting along the shore.

Foxes and wolves were present at the time, but even if they could produce the type of specimens found, it seems unlikely that mammalian predators of this type would be persistently successful in killing Shelduck, or would have transported them for long distances overland. Two avian predators large enough to have taken such prey are known from the Tornewton Cave – the Eagle-owl and the White-tailed Sea-eagle. The former is unlikely to have moved very far from the cave to hunt, and may have concentrated mainly on mammalian prey. The Sea-eagle, however, usually hunts and scavenges on seacoasts, taking numbers of ducks and larger waterfowl. The Shelduck, which is conspicuous at a distance, feeds on mudflats where it cannot dive to avoid a winged predator, and is fairly slow to take flight, would be a natural prey for the eagle. Sea-eagles are not normally cave-nesters and it is not obvious how they would have utilized the Tornewton site. It is possible that the rock platform at the top entrance might have formed a nest site from which food and pellets could have fallen into the cave.

Shelduck remains, although numerous from the Glutton to the Hyaena Strata at Tornewton, are suddenly absent in the Devensian. This could suggest a change in species distribution, but since prey remains in caves are determined by the species of raptor present it could alternatively indicate a change in the latter. The Brixham Devensian material consists almost entirely of Shelducks, indicating that the species was certainly present for at least part of this period. An absence of the Sea-eagle from Tornewton Cave in the Devensian period, possibly coincident with the use of the cave by man, is likely to have been why the Shelduck bones are absent, rather than a temporary absence of the latter species from this region. Since the larger prey are typical of the Sea-eagle it may be significant that during the Devensian the only waterfowl remains at Tornewton are those of the very small Teal.

The Common Buzzard of the Brixham Cave may have been there by accident or as a prey item rather than a predator. It is just possible that this species might have utilized a cave in a very bare and windswept biotope, but in inland areas it would normally have used trees where these were available, or the ledges of larger rock outcrops, for roosting and nesting.

The Kestrel was present at Tornewton in the earlier cold period and the interglacial and may well have been responsible for the presence of small passerine bird remains as well as those of small mammals. Other species of falcon tend to concentrate almost entirely on birds. Other raptors which produce small bird bones in prey remains are the small to medium-sized owls, of which there is no evidence in the material from Tornewton, although the presence of the remains of prey without those of the predator is not unusual where birds are concerned. There are no Kestrel remains from the Devensian strata but the presence of small passerine remains from this period suggests that this or a similar smallish raptor was present.

The species list as evidence of climate

Since there is evidence of climatic variation from one stratum to another in this cave material, and since this is reflected in the mammal species present, similar changes in the bird fossils could be expected. In fact, within this group the situation is more complicated because of the greater mobility of birds. Resident bird species give some indication of the conditions at the time, but within this region the majority of birds are partly or wholly migratory. The presence during a cold period of a species which can tolerate the warmer summer conditions, combined with the presence in a warmer period of cold-adapted species wintering in the area, can seriously confuse the general picture which bird fossil may provide. There is some evidence of this problem in the present material.

Of the species present in the earlier cold Glutton to Otter Strata, the White-tailed Sea-eagle, Kestrel, Eagle-owl, Crow and Raven are now resident from the temperate zone at least as far as the northern edges of the Boreal forest zone and may extend into wooded tundra (climatic zones as in Voous 1960). The Brent Goose and Goosander have a similar range but make a more southerly shift to warmer boreal and temperate parts in winter. The Shelduck has a mainly warm temperate distribution at the present time but on the eastern Atlantic seaboard extends north to northern Norway. This is correlated with the presence of the warm North Atlantic Drift current modifying sea and shore temperatures, although in the Scandinavian part of its range the species is only a summer visitor. The Western Partridge is a member of a genus of gamebirds normally found in warm temperate to temperate zones, although the Rock Partridge and Chukar will ascend to fairly high altitudes.

The two stork species are now summer visitors to Europe, nesting as far north as northern Denmark and the Gulf of Finland, and Voous (1960) suggests that the northern limit of their range is correlated with the July isotherm of 62 °F (16·7° C). The final species recorded for this period is the Crossbill, and the occurrence of this species, unless it was a dying stray from some irruptive movement, would indicate the nearby presence of conifer trees.

If it is reasonable to view this material as an entity, it suggests that during this early cold period the surroundings of the cave might have resembled present-day southern Scandinavian boreal conditions, with the presence of some conifer trees and a mid-summer temperature of *c.* 62 °F. However, the winters might have been more severe (Sutcliffe & Zeuner 1962).

The species present in the Hyaena Stratum in the warmer interglacial are disappointing as climatic indicators. The list could be one indicating birds now present in a temperate zone in winter or a boreal zone in summer. The only exception is the tentatively-identified Ruddy Shelduck. This is mainly a species of drier steppe regions. The Starling may have roosted and nested in the cave. The presence of both the latter species and the Skylark suggests that some open grassland was present nearby.

For the Devensian period, the presence of the Arctic/Alpine Ptarmigan indicates more definitely a colder climate. The Willow Grouse might have been the typical bird of cold willow and birch scrub, or possibly a Red Grouse form adapting to heather moorland. The grassland Starling and Skylark were still present. Of the remaining species, Teal, Fieldfare and Crow are all species that might occur from temperate to subarctic conditions, but are not tundra birds. The exceptional occurrence is the Little Bustard. This is a warm temperate species, extending into temperate regions in summer, and at present just reaching northern France. It is, however, partly a migrant, and it is possible that the Tornewton specimen was a stray individual that had overshot its usual range at that time. At Brixham, the combination of Common Buzzard and Shelduck suggests boreal rather than tundra conditions.

Sutcliffe & Kowalski (1976) have over 2000 specimens of rodents from Tornewton Cave and with this more abundant material have produced a table of the relative proportions of the various groups of rodents, part of which is shown in Table 2. It will be seen that they also found evidence of boreal and forest species in the colder periods. Except for the presence of the Ptarmigan in the Devensian, the tundra element cannot be confirmed among the birds.

Table 2 Relative proportions of the various ecologic groups of rodents found in Tornewton Cave (from Sutcliffe & Kowalski 1976:66)

Layer	Tundra and steppe	Boreal	Forest	Neutral
Reindeer Stratum	22·9	8·7	5·5	62·8
Hyaena Stratum	0	0	2·3	97·7
Bear Stratum	25·8	48·4	9·6	16·1
Glutton Stratum	22·7	64·2	0·7	12·4

It is possible that the higher ground of Dartmoor and similar moorland areas could have carried a tundra-type fauna and flora when more sheltered areas of lower ground might have had a more boreal flora with some trees, as in parts of northern Scandinavia today. It also seems possible that this area of south-west England, on the southern side of higher ground and close to an oceanic shoreline, might have experienced, even under severe conditions and at different stages of sea-level, a more favourable climate compared with sites further inland on the continental landmass. These opposite tendencies could have resulted in a more varied fauna and flora at these earlier periods in this area.

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